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Courtship lateralization and its effect on mating success of male wild turkeys (Meleagris gallopavo)

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Courtship lateralization and its affect on mating success of male wild turkeys

(*Meleagris gallopavo*)

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ABSTRACT

Mara E. Vernier: Courtship lateralization and its effect on mating success of male wild turkeys (*Meleagris gallopavo*)
(Under the direction of Richard Buchholz)

Lateralization results from unequal processing of tasks in the different hemispheres of the brain. While lateralization is a widely researched topic of study, little is known about the effects of sexual selection on lateralization. The purpose of this study was to determine if there is lateralization of male wild turkey (*Meleagris gallopavo)* courtship and whether the presence of lateralization is associated with male mating success. Male behavioral data were collected from video recordings of courtship made by Dr. Richard Buchholz during a previous mating study. Males were categorized as either successful or unsuccessful males based on how often they were chosen by females during 173 mate choice trials. In order to assess if lateralization of courtship exists, the side (left or right) used by each male while courting the hens was recorded and quantified. My results reveal that population level lateralization does not occur in the courtship of male wild turkeys. Individual lateralization, however, was present in the majority of tested males. The most strongly lateralized males had the highest mating success. Strength of lateralization may allow females to assess male fitness in order to choose the best mate.

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INTRODUCTION

Laterality is an evolved difference in the two hemispheres of the brain resulting in unequal function both behaviorally and physiologically (Franklin III et al., 2001). Laterality has given organisms the ability to specialize each hemisphere for different tasks and behaviors in order to increase efficiency and coordination. For example, laterality of foot use in parrots and handedness in humans enables increased dexterity in picking up and holding objects on one side of the body as opposed to the other (Franklin III et al., 2001). However, lateralization is not limited to the use of limbs; it has also been observed in escape behaviors and eye use in fish as well as birds (Franklin III et al., 2001). Because of the limitations of binocular visual range due to eye placement, bird visual lateralization is frequently studied (Rogers, 2012). Visual lateralization has been recognized as a significant effector in certain survival tasks, such as foraging and predator detection, as well as mate choice. However, visual lateralization has not been described in terms of a courtship display in relation to mate choice.

Courtship displays are a way of showing off morphological and behavioral characteristics in hopes of attracting the opposite sex. It is believed that male courtship display is used by females to assess the quality of the male (Fusani et al., 2014). A male wild turkey (***Meleagris gallopavo*)** performs a courtship display known as "strutting" during which he can only display one side to the female at a time (Dickson, 1992). Visual and side bias (i.e., lateralization) of courtship in the wild turkey could affect mating success of males. The purpose of my research was to determine if there is lateralization of

male turkey courtship and whether lateralization correlates positively with male mating success.

In the following background information, I explore the theory of sexual selection, the origin of lateralization, and how the anatomical structure of birds is particularly suited for the study of cerebral lateralization. Lateralization has the potential to expand our understanding of interspecific variation in avian courtship patterns.

BACKROUND INFORMATION

Sexual Selection

Sadava (2011) defines sexual selection as acting upon characteristics that influence reproductive success. While these characteristics may not increase the organism's chance of survival, they do affect the chances of mating. Sexual selection is further divided into two categories: intrasexual selection and intersexual selection (Darwin, 1871 in Sadava et al., 2011). Intrasexual selection refers to characteristics that aid the organism to better compete with members of the same sex for potential mates. On the other hand, intersexual selection refers to characteristics that aid the organism to attract more members of the opposite sex. Likewise, Trivers (1972) elaborates in most species the competition is between males for mating privileges with females and the females are the "chooser" of a mate. It is argued that this is due to the energetic investment each sex contributes to an individual offspring (Bateman, 1948 in Trivers, 1972). Females have more energetic investment in each gamete and often spend more time performing parental care, thus one limiting factor of female reproductive success is the availability of nutrients. The limiting factor in reproductive success in males is mate availability (Berenstain et al., 1983), because sperm are inexpensive to produce compared to eggs.

While in some species females benefit directly when males help to care for offspring, females of non-resource-based polygynous species do not receive these benefits (Sardell et al., 2014). Polygynous species, such as the wild turkey, mate with more than one individual in a breeding season. However, these females still receive indirect genetic benefits from their mates, such as alleles that increase offspring survival

(Sardell et al., 2014). With indirect benefits as the only outcome of non-resource-based mate choice, females have become more selective for good genes as compared to resource based mate choice, ensuring a higher rate of survival for their offspring. There are many aspects of sexual selection that have not yet been explored. Lateralization could be a "good gene" that aids sexual selection in turkeys. If lateralization is considered a "good gene", hens would benefit by having offspring that are lateralized. The general basis of lateralization in a variety of species is explained below.

Lateralization

It could be argued that lateralized individuals have an advantage in sexual selection (Rogers and Andrews, 2002). Lateralization exists in most vertebrates, including birds and reptiles (Koboroff et al., 2008). The statistical pattern of lateralization within species varies and can be categorized either as individualized lateralization or population wide lateralization (Rogers and Andrew, 2002).

Individualized lateralization corresponds to different individuals in the population being lateralized to the left or right, but the population as a whole does not have a specific lateralization bias. Mice and rats are individually lateralized in food retrieval; half of the population is right handed and half of the population is left handed (Collins, 1985 in Rogers and Andrews, 2002). Lateralization for food retrieval was developed in each individual, but the entire species does not have a common side of lateralization. The development of individualized lateralization could be an advantage for reducing predation risk; a population wide laterality would result in predictability of the prey leading to decreased survival. Predictability of population lateralization would allow

predators to observe prey behavior and determine a population wide side of vulnerability for attack.

Population wide lateralization occurs when all of the individuals within a population are lateralized in the same way, meaning there is a bias towards one side. An example of this statistical pattern is seen in lower primates, such as prosimians, as the population has a left handed bias towards food holding but a right handed bias towards holding onto branches (Ward et al., 1993 in Rogers and Andrews, 2002). Population wide biases most likely stem from social pressures causing learned behaviors in young. For example, young chicks exposed to light before hatching develop visual lateralization with a population bias that results in a more stable social hierarchy than young chicks that were hatched in the dark and do not have a bias. Lateral eye placement in birds affects the visual field in ways that make lateralization more likely.

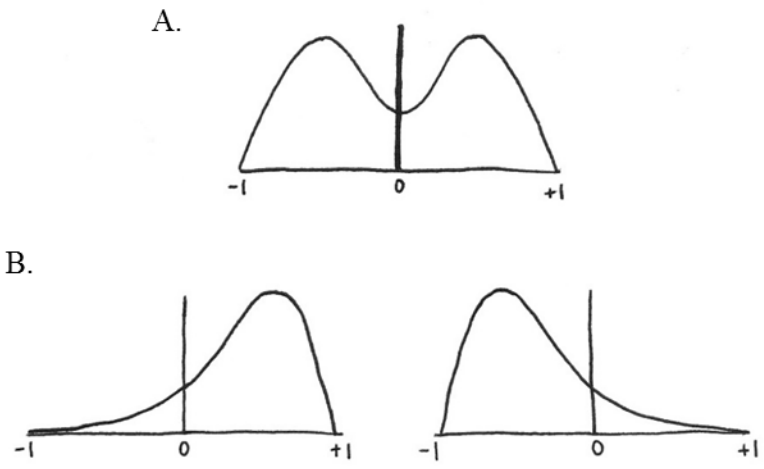

Figure 1. (A) Individual and (B) population lateralization. Population lateralization results in most individuals within the population being lateralized to one side, where as individual lateralization has both variations equally. -1 indicates left lateralization, 0 indicates no lateralization, and +1 indicates right lateralization. Modified from Figure 1.3 (Rogers et al. 2013).

Avian Visual Fields

Due to the lateralized eye placement of most avian species, the maximum binocular field is limited to only 20-30° in front of the bird's beak (Martin, 2007). The majority of the avian field of view is monocular. Thus, for the most part, a bird simultaneously views two different visual fields, each with a different eye. To account for these two different stimuli, birds have the ability to move each eye independently (Rogers, 2012). Lateral eye placement along with specialized eye movement limits the field of total blindness, which is the area around the circumference of a bird's head that cannot be viewed by either eye. Lateral eye placement makes for better predator detection.

The degree of frontal overlap depends on the type of bird and their primary eye use. For example, the large degree of frontal overlap in an owl is uncommon for an avian species. The eye placement of an owl is due to large ear holes present on the sides of the owl's head (Figure 1). The owl uses its sense of highly developed hearing more than its sight to listen for prey and for predators behind and around it. Conversely, the turkey has a small degree of frontal overlap and a large monocular field because bill placement obscures the forward visual field (Martin, 2007). With primarily monocular vision, the turkey must often choose only one eye to observe an object (Figure 1). The repetition of choosing a certain eye for one task leads to the familiarity of that side of the brain of viewing a specific object, which is how specialization in the different hemispheres occurs. Unique structures of the avian brain, as described in the following section, explain how hemispheric specialization occurs.

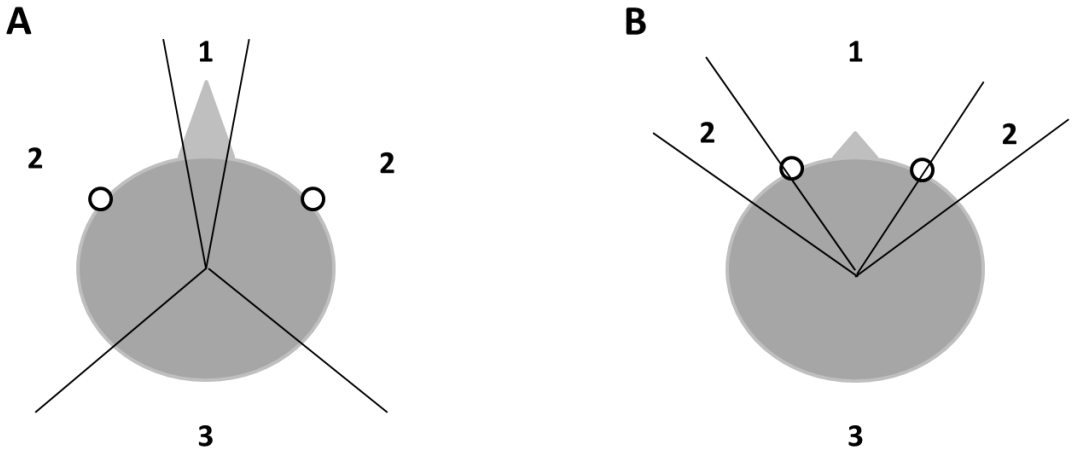

Figure 2. Visual fields of (A) turkey and (B) owl. White circles denote eye placement and numbers represent field of vision for each species: 1) binocular, 2) monocular, and 3) not within field of vision

Avian Brain Structure

The function of laterality is evident when observing avian brain structure in relation to eye placement. Optic nerves in these species are linked contralaterally to the different brain hemispheres, thus linking eye use to cerebral lateralization (Franklin III et al., 2001). Experimentation has demonstrated that the left and right hemispheres process visual stimuli differently and therefore produce a different response depending on the eye used (Rogers, 2012).

There are two reasons why birds have a drastic difference in response depending on eye use as opposed more weakly lateralized vertebrates. The first reason is that birds lack a corpus callosum, which transfers stimulus from one hemisphere to the other in mammals (Prior et al., 2008). Studies of the corpus callosum in humans revealed that the larger the corpus callosum, the less lateralized the individual (Luders et al., 2010). A larger corpus callosum allows increased communication between the hemispheres of the brain. Without the corpus callosum, birds can only transfer information via the supraoptic

decussation, which is slower in communicating (Templeton et al., 2012). Lower speeds of hemispheric communication in avian species heighten the degree of hemispheric asymmetry and make the choice of eye recruitment essential. Loss of the use of one eye could cause a decline in the survival abilities of an individual. Second, the number of projections coming from each eye to the forebrain in birds differs; the right eye having twice as many projections as the left, which causes different signal intensity sent from each eye (Rogers, 2012). Studies of eye use have been conducted to determine the occurrence of lateralization for certain tasks. The next section outlines a variety of avian species and their preferential eye choice in different situations.

Avian Processing Asymmetries

Brain anatomy and eye placement in birds result in the neural processing of certain tasks to be particularly "one sided". Thus birds should perform specific tasks less successfully using one side of the brain as opposed to the other. While there is not always a population wide side bias in birds for every function, Table 1 outlines some bird species and their hemispheric preferences. The strength of lateralization, however, may explain more about function than the side of the lateralization (Reddon et al., 2009).

Strongly lateralized individuals possess the advantage of multitasking (Dharmaretnam et al., 2005). Evidence of this advantage was seen in chicks (*Gallus domesticus*) participating in foraging and predator detection simultaneously. Strongly lateralized individuals were able to distinguish between food and pebbles with the left eye while scanning for predators with the right eye. However, when monocular vision was tested, lateralized individuals were only able to successfully complete one of the two tasks depending on the eye used. Conversely, weakly lateralized individuals were not as

efficient in multitasking. However, when monocular vision was tested their success in each task remained the same. When each task was tested individually, the level of success for strongly and weakly lateralized individuals was identical.

Weakly lateralized individuals are less vulnerable to predation than strongly lateralized individuals (Reddon et al., 2009). Statistically speaking, events are equally likely to occur on both sides of the body, so strongly lateralized individuals are at a disadvantage if predation occurs on the side not specialized for predator detection. While weakly lateralized individuals are not as proficient at predator detection, they are able to perform predator detection with both eyes.

If the task proficiency benefits of lateralization shown for foraging and predator-avoidance translate to benefits in the context of reproductive behavior, the courtship of strongly lateralized individuals should be more successful at attracting mates, as they will be more proficient in the process of courting females.

Table 1a. Review of avian hemispheric specialization studies with left side bias.

Hemisphere Used	Context	Species	Explanation	Study
Left	Predator Detection	Juncos	Use the right eye primarily to scan for predators	Franklin III et al. 2001
Left	Mate-choice: coloration	Gouldian finch	Males are mate choice biased only with right eye	Templeton et al. 2012
Left	Social Stimulus: positive	Quail	Use right eye when approached by a companion	Zucca et al. 2008
Left	Visual information processing	Australian magpies	Used to process visual information prior to approaching a predator and prior to withdrawing from it	Koboroff et al. 2008
Left	Learning: food discrimination	Pigeons	Were able to learn faster when using their right eyes and were then able to reach higher performance levels	Verhaal et al. 2012
Left	Categorization	Domestic chickens	Categorizes stimuli based on common features and used for quick decision making	Rogers 1996
Left	Learning: food discrimination	Domestic chickens	Follow established rules put into place by past experiences, leads to the ability to focus on relevant information and avoid distraction.	Rogers 2008

Table 1b. Review of avian hemispheric specialization studies with right side bias.

Right	Agonistic Response	Australian magpies	Used when circling and mobbing a predator, high alert inspection of a predator	Koboroff et al. 2008
Right	Predator Detection	Tree sparrows	Used primarily to scan for predators	Franklin III et al. 2001
Right	Side Lateralization	Quail	Turn preferentially leftward	Zucca et al. 2008
Right	Social Stimulus: negative	Quail	Use left eye when approached by a stranger	Zucca et al. 2008
Right	Spatial Differentiation	Domestic chickens	Used to determine location using topographical clues	Rogers 1996
Right	Social stimulus	Domestic chickens	Used to distinguish between known and unknown. Approached a familiar chick and avoided an unfamiliar one	Rogers 2008
Right	Agonistic Response	Domestic chickens	Heightened levels of aggression and copulation when the left eye is used	Rogers 2008

Objectives

The purpose of my research is to determine if lateralization of courtship is associated with male mating success in wild turkeys. My null hypothesis states there is no lateralization of courtship, and therefore the eye use of the individual males during courtship is equal. My alternative hypothesis states that the laterality of courtship is sexually selected by females. Although the sexual selection hypothesis does not predict a preferred side for male courtship displays (i.e., a population bias), this hypothesis does predict that a) biased males will be more likely to mate, and b) the strength of lateralization will correlate positively with mating success.

METHODS

STUDY SPECIES

Dickson (1992) outlines the basic biology of the study species, the wild turkey (*Meleagris gallopavo).* The wild turkey is a gallinaceous bird native to the North American Continent. It is either placed in its own family, Meleagrididae, or as a subfamily in the larger family of Phasianidae, of the order Galliformes. Some other gallinaceous birds within this family include chicken, quail, and peafowl. However, the wild turkey is most closely related to the pheasant.

Meleagris gallopavo is a sexually dimorphic species, meaning that the males and females develop morphological differences in addition to their reproductive differences. Some of these characteristics include color and size of the birds and can be seen as early as four months of age. The feather color or plumage of the female turkey, the hen, is duller than that of the male turkey, the gobbler. The hen's plumage is often a light shade of brown whereas the plumage of the gobbler is darker and blacker.

The males each mate with multiple females and have no responsibilities of parental care for their offspring. Therefore, the only limit to the amount of offspring they can have during one mating season is their number of copulations. Thus, males mate with as many females as possible.

Experimental Design

Male wild turkeys, *Meleagris gallopavo*, were hatched at the University of Mississippi Field Station in the Department of Biology's Avian Research Facility in 2007

for a study done by Dr. Richard Buchholz on the effects of female parasitism on mate choice. Dr. Buchholz recorded mating trials on video tape in 2009. I used the footage for my observations of the laterality of male turkey courtship display.

The mate choice arena was a large caged area divided into two sections (Figure 2). One section housed the males, and the other was the female choice section. In the male section there were sixteen male turkeys housed separately in adjacent cages. The walls between adjacent cages were opaque so that the males were unable to see one another. There were eight video cameras, each with a view of two adjacent male cages as well as the female choice section directly in front of these cages. The video captured all male activity during the trials regardless of whether the female was present in the range of view.

During the trials one female was allowed in the viewing area for a maximum of thirty minutes. If the female chose to solicit a male for a total of five minutes continuously, the trial was ended early. If the female seemed to be in distress during the trial, or exhibited abnormal behavior, the trial was also ended early.

To analyze the male behavior in these trials, I used a free program called Jwatcher (www.jwatcher.ucla.edu) for the behavioral analysis of animals. The program allows customization of key strokes by the user for their specific studies (Blumstein and Daniel, 2007).

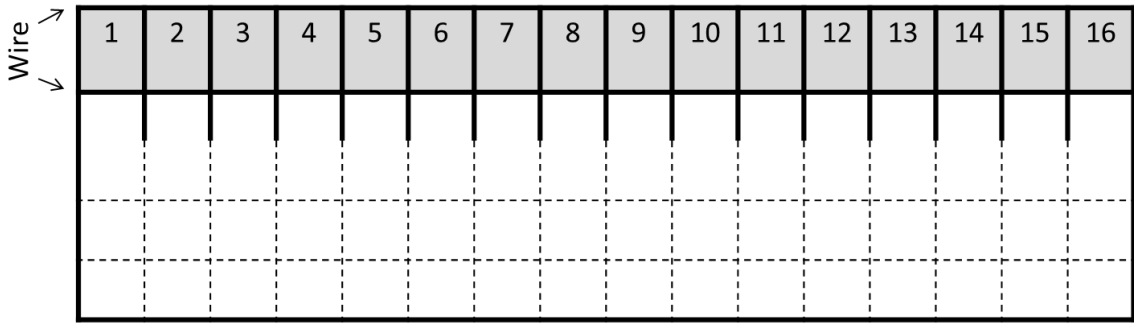

Figure 3. The mate choice arena. The gray boxes numbered 1 through 16 represent individual 2 x 1.5m male cages. The barrier between the adjacent male cages was extended into the female section of the arena, preventing the females from viewing more than one male at a time. The white 1.5m wide range is the female choice area, divided into three horizontal zones for female position documentation during the mating trials.

MALE BEHAVIORAL DATA COLLECTION

In order to determine if lateralization during courtship correlates with increased mating success, males were separated into two subgroups (high and low) based on the number of females that chose to "fully solicit" males. Males with more than three solicits were placed in the high subgroup and males with three or less solicits were placed in the low subgroup. A "full solicit" corresponds to five minutes of the female engaging in an uninterrupted crouch position, indicative of mate choice.

A subsample of each male's 173 trials was observed for laterality. Starting with trial one, trials were examined sequentially until one was found where the male displayed for at least 5 minutes. Then the next 4 trials were skipped and trials were examined sequentially until another was found with 5 minutes of display, and so on for all trials of each male.

The degree of lateralization present during courtship of each individual male was measured from the videotaped trials. The description of male courtship action patterns is present in Table 2. Starting when the male began the courtship ritual in the position

known as “full tail” or “display”, the eye used to look at the female was recorded. This process was continued in each trial until five minutes of full tail was observed in total.

Table 2. The behavioral actions recorded for the males

Behavior	**Definition**
Half Tail	The feathers of the tail are not fully fanned
Full Tail	The feathers of the tail are fully fanned out for display to the female
Strutting	A series of quick steps taken with the wings dropped down and dragged with the tail in full extension. An audible sound is produced by vibrating the trachea

STATISTICAL ANALYSIS

The degree of lateralization for individual males was calculated as follows:

$$\text{LE percentage} = \frac{\text{Display time using LE (sec)}}{\text{Display time LE+ Display time RE (sec)}} \times 100$$

Where LE = left eye and RE = right eye.

LE percentages in each trial were averaged for each male to determine individual percent of lateralization. Standard error (SE) was calculated for the means. To determine if individual lateralization occurred, the data for each male were analyzed using a two tailed one sample t-test to determine if the mean was different from the expected value of 50 percent, which is equal use of both eyes. Population lateralization of each subgroup was found by averaging the individual degree of lateralization of each male. To determine if population lateralization of courtship occurred, the data for each subgroup were analyzed using a two tailed t-test to determine if the mean was different from the expected value, which would be equal use of both eyes by all individuals. Population lateralization average of each subgroup was then compared using a two sample t-test. Strength of

lateralization refers to the absolute value of the difference between mean and equal eye use (50% LE percentage). Average strength of lateralization of each subgroup was found. Comparisons between the two groups were made by using a two sample t-test to determine differences between the subgroup means. Simple linear regression was used to determine an association between individual strength of lateralization with mating success. Strutting averages per subgroup were calculated and standard error was found. P-values ≤ 0.05 were considered statistically significant. T-tests were conducted online at www.biostathandbook.com.

RESULTS

There was no population-level lateralization of male courtship ($\bar{x}$ ± SE = 50.63 ± 2.1, t= 0.30, df = 9, p > 0.05). Six out of the ten males showed a significant individual side bias during courtship (Figure 3, Appendix I), however. Four males exhibited a significant left side bias, two exhibited a significant right side bias, and the remainder showed no side bias. The group of males with high mating success exhibited a greater range of mean left side use (23.48) than the low mating success male group (9.64), but neither group showed a significant directional bias (Figure 4; low: $\bar{x}$ ± SE = 49.75± 1.7, t= 0.143, df = 4, p = 0.89, and high: $\bar{x}$ ± SE = 51.51± 4.0, t= 0.378, df = 4, p = 0.72). Left side use did not differ significantly between the two male groups (t= 0.404, df = 4, p > 0.05).

The strength of lateralization, on the other hand, was significantly different than zero in both low ($\bar{x}$ ± SE = 3.07± 0.8, t= 3.78, df = 4, p = 0.02) and high ($\bar{x}$ ± SE = 7.13± 1.9, t= 3.69, df = 4, p = 0.02) mating success groups. The difference in strength of lateralization between male groups did not reach statistical significance (t= 1.94, df = 4, p = 0.09). The strength of lateralization was positively associated with mating success (R^2= 0.517, n=10, P=0.011; Figure 7). Most males were fairly consistent with their strength of lateralization across the breeding season, but one individual showed a dramatic increase in strength, while another male showed notable weakening of lateralization during this time frame (Figure 8). The rate of strutting was equivalent in the two male groups (low: $\bar{x}$ ± SE = 12.21± 2.6, and high: $\bar{x}$ ± SE = 14.31 ± 2.0), and thus did not explain male mating success (t= 0.64, df = 4, p > 0.05).

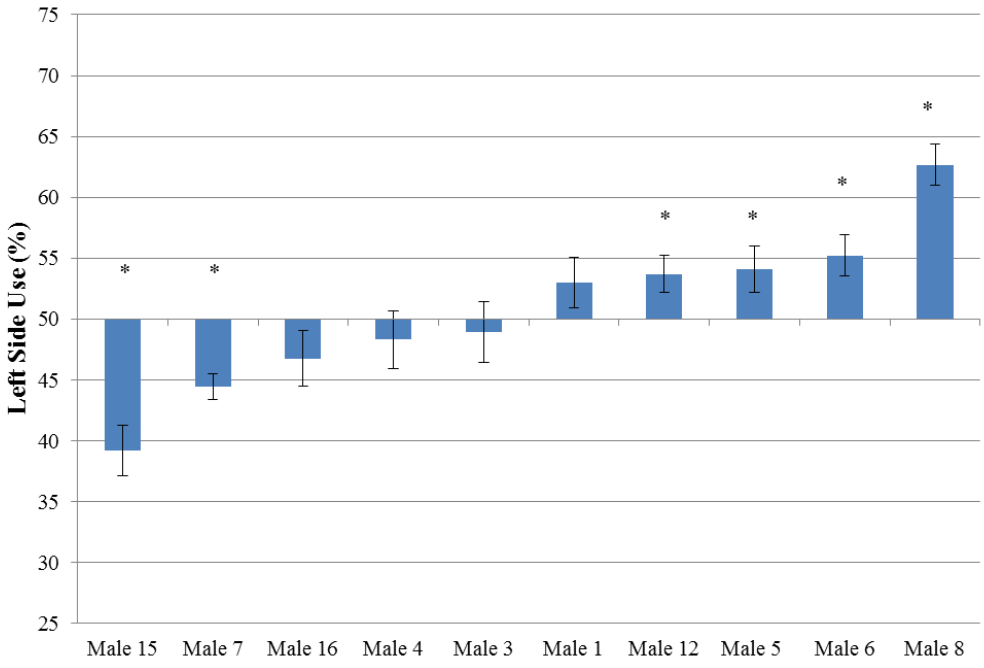

Figure 4. Percent side use during courtship of 10 individual male wild turkeys. Birds are listed from most right biased to most left biased. Individuals showing significant lateralization are marked with an asterick ($p \leq 0.05$)

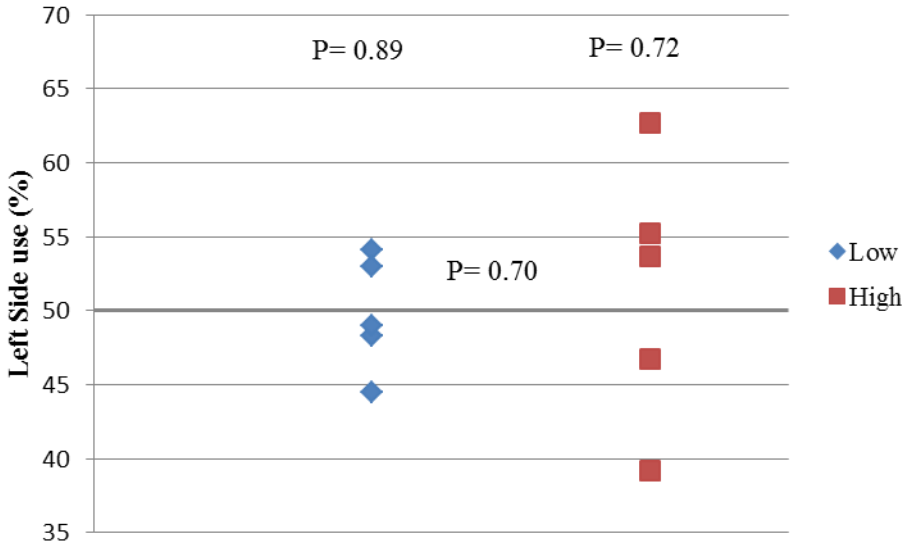

Figure 5. Population lateralization and mating success in low (N=5) and high (N=5) subgroups, calculated from left eye preference. 50% indicates equal eye use.

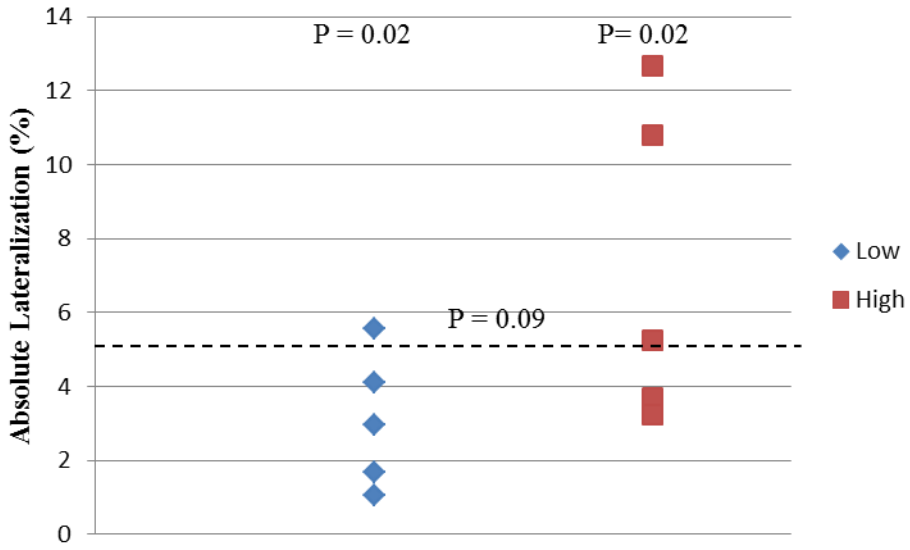

Figure 6. Lateralization strength and mating success in low (N=5) and high (N=5) subgroups. Lateralization percent quantifies deviation from equal eye use. Dashed line indicates entire population mean.

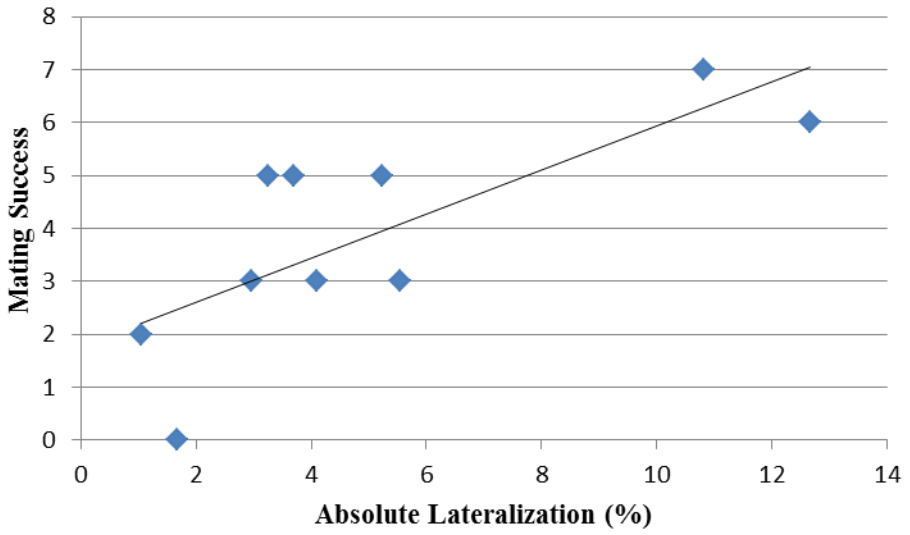

Figure 7. Display lateralization was positively correlated with male mating success ($R^2 = 0.5713$, $p = 0.011$)

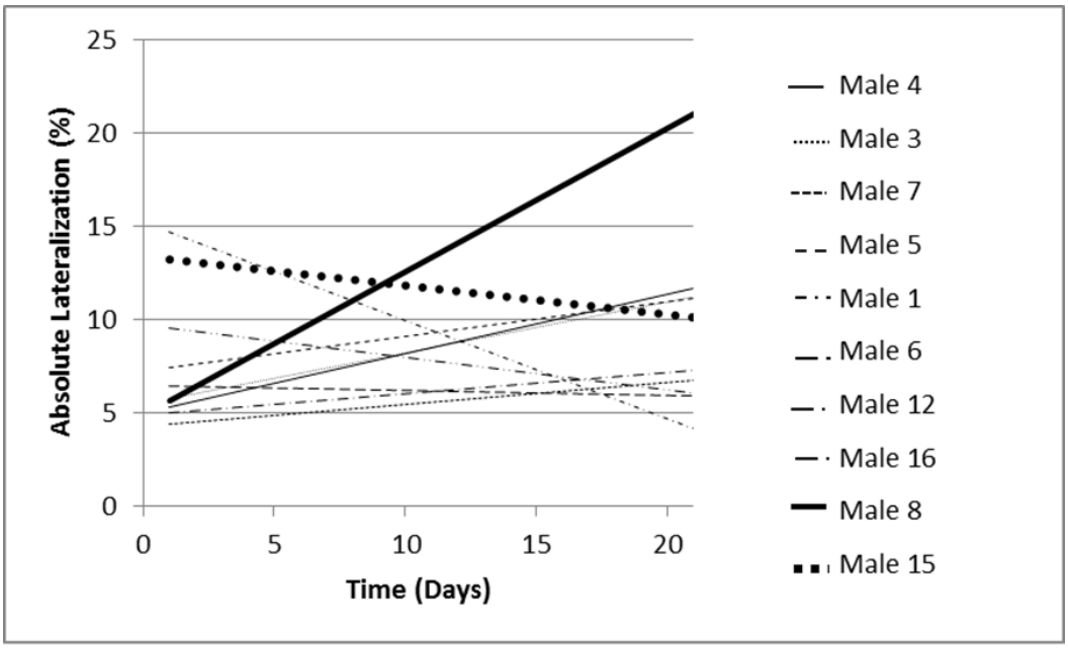

Figure 8. The strength of lateralization is relatively constant over the length of the breeding season in most males.

DISCUSSION

Lateralization plays an important role in increasing task efficiency in a variety of species (Rogers and Andrews, 2002). Avian species in particular benefit from the use of lateralization to avoid predation, improve foraging, and engage in mate choice (Dharmaretnam et al., 2005; Templeton et al. 2012). Few studies explore the role of lateralization in sexual selection despite the importance of side bias to intrasexual conflict, courtship display production, and assessment (Krakauer et al., 2016). My results help us understand how sexual selection is influenced by lateralization and give insight into the role of brain hemispheric specialization for mating success.

Population lateralization has been documented in a variety of avian species (Templeton et al., 2012). My research, however, shows there is no unidirectional population lateralization of courtship among the male wild turkeys that I studied. This result is surprising given that Romano et al. (2015) concluded that population lateralization is common among avian species. For example, population level lateralization of male courtship was seen in both sage grouse (Krakauer et al., 2016) and zebra finches (Workman and Andrew, 1986 in Templeton et al., 2012). Interestingly, sage grouse varied in mating success depending on strength of lateralization similar to the way my study subjects behaved. I conclude that neither brain hemisphere is pre-adapted for eye use during courtship, but the advantages of lateralization are still present at an individual level even with the absence of population level lateralization. As previously

stated, in certain contexts (such as fighting or predator avoidance) the predictable nature of population lateralization becomes a disadvantage (Vallortigara and Bisazza, 2002).

Across species and motor tasks, individual lateralization may be seen either in concert with population lateralization, or independent of it. Interspecific variation in the occurrence of both population and individual lateralization gives credence to Vallortigara's (2005) argument that lateralization gives organisms certain task specific advantages. Unfortunately the relative advantages of the two levels of lateralization remain unclear, in part because individual lateralization has rarely been studied in birds. During wild turkey courtship, I showed that, as predicted, individual lateralization of courtship existed in the majority of tested males. In another bird species, the New Caledonian crow, individual lateralization for tool use occurs with varying strength of lateralization (Martinho et al., 2014 in Romano et al., 2015). It is interesting that although no universal side bias was observed in my studied population, there was considerable variation in the strength of lateralization among individuals, and it was the strength of side bias that explain male mating success. The data obtained by studying New Caledonian crows as well as the results found in my study is in accordance with the Reddon (2009) hypothesis, which states that the individual variation of strength of lateralization could explain the fitness outcomes of variation of behavior.

Perhaps variation in lateralization is maintained by natural and sexual selection because strong lateralization is beneficial for multitasking while weak lateralization leads to less vulnerability from predation (Dharmaretnam and Rogers., 2005; Reddon et al. 2009). It remains unclear why female turkeys favor strongly lateralized males. This male trait could increase the survival of their offspring if side bias indicates some indirect

genetic benefit to females (Sadava et al., 2011), but the exact mechanism of this benefit to turkey hens is unclear. It is possible that females derive no benefit from choosing lateralized mates, but merely are more stimulated by males that have more effective displays due to hemispheric specialization. Mate preference due to a sensory bias of females towards certain male display characteristics have been described in other study systems. For example, female swordtail fish (Xiphophorus helleri) prefer longer-sworded males without gaining "good genes" for offspring survival by mating with them (Basolo, 1990).

Although individual males were significantly lateralized on average, the degree of lateralization for some strengthened or weakened across the breeding season. I can think of two possible interpretations of these patterns. First, individual males may learn from the female responses to their display and adjust their courtship to maximize interest by the choosy hens. Second, there might be a physiological cost to always using one side of their body for display. Perhaps some strongly lateralized males exhaust their muscles as time progresses. Both of my explanations may occur simultaneously to explain the variation in strengthening and weakening of lateralization in different males.

Intersexual selection, a type of sexual selection, refers to characteristics that make the organism more favorable to potential mates (Darwin, 1871). Sexual selection acts on characteristics that increase mating success of individuals, but not necessarily of both parties involved in copulation. The results of my study support the idea that lateralization of male courtship is favored by sexual selection.

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APPENDIX I

Mean percent side use during courtship of 10 individual male wild turkeys. Values above 50% are left biased and those below 50% are right biased.

	Male 15	Male 7	Male 16	Male 4	Male 3	Male 1	Male 12	Male 5	Male 6	Male 8
Mean (%)	39.191	44.4446	46.7526	48.3163	48.9463	52.9698	53.6901	54.0877	55.2342	62.6709
Standard Error	2.06488	1.08283	2.28496	2.38344	2.4845	2.06152	1.54195	1.91331	1.71625	1.67485
N	31	32	28	29	27	32	34	31	34	31
t-value	5.2347	5.13044	1.4212	0.70643	0.86381	1.44057	2.39313	2.13645	3.04978	7.56541
p-value	1.2E-05	1.5E-05	0.16671	0.48576	0.39503	0.15973	0.02255	0.04092	0.00449	2E-08